Title: Morphological divergence in giant fossil dormice

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Abstract

Insular gigantism – evolutionary increases in body size from small-bodied mainland ancestors - is a conceptually significant, but poorly studied, evolutionary phenomenon. Gigantism is widespread on Mediterranean islands, particularly among fossil and extant dormice. These include an extant giant population of *Eliomys quercinus* on Formentera, the giant Balearic genus †*Hypnomys* and the exceptionally large †*Leithia melitensis* of Pleistocene Sicily. We quantified patterns of cranial and mandibular shape and their relationships to head size (allometry) among mainland and insular dormouse populations, asking to what extent the morphology of island giants is explained by allometry. We find that gigantism in dormice is not simply an extrapolation of the allometric trajectory of their mainland relatives. Instead, a large portion of their distinctive cranial and mandibular morphology resulted from population- or species-specific evolutionary shape changes. Our findings suggest that body size increases in insular giant dormice were accompanied by evolutionary divergence of feeding adaptations. This complements other evidence of ecological divergence in these taxa, which span predominantly faunivorous to herbivorous diets. Our findings suggest that insular gigantism involves context-dependent phenotypic modifications, underscoring the highly distinctive nature of island faunas.

Keywords

Insular Gigantism; Geometric morphometrics; Allometry; Island rule; *Leithia*; *Hypnomys*

Introduction

Insular gigantism is a widespread macroevolutionary pattern [1,2]. It occurred on many Mediterranean islands throughout the Neogene and Quaternary, and is known among small mammals including dormice, hamsters, murids, lagomorphs, shrews and moonrats [3-10]. Despite its prevalence, the ecological drivers of insular gigantism are rather complex, with climate, island area, availability of

resources, and the presence of competitors and predators all proposed to play a part [2, 11-18]. Similarly, the morphological consequences of gigantism are not well understood, and it is not clear whether giant island species have attained large size via similar evolutionary pathways. This raises the possibility that insular gigantism does not represent a single well-defined process, but in fact reflects the outcomes of evolution in a broad set of distinct ecological contexts.

Shape changes associated with increasing body size (allometry) are suggested to either result from optimised functionality based on natural selection, or from constraints that impose fixed or slowly-evolving allometric trajectories [19]. Allometric constraints will result in shared allometric patterns ('common allometry') among related species, and provide an expectation that evolution will proceed along lines of least evolutionary resistance (or "genetic lines of least evolutionary resistance") [20], represented by a multivariate factor of the genetic or phenotypic variation [21] (but see [22]). Deviation from these lines might be expected during adaptation to distinct ecological niches, resulting in functional modification in shape and size. However, the evolvability of allometric relationships, and therefore the ability of ecological adaptation to cause divergent patterns of phenotypic evolution, is variable [23,24]: divergence from allometric trajectories may be common on long macroevolutionary timescales but are rare on shorter timescales.

The Island Rule describes extensive variation in both shape and size [1], and suggests a graded trend from gigantism in small mammals to dwarfism in larger species [13]. The evolutionary timescales of adaptation to insularity are generally short [25], meaning that divergence from an ancestral allometric trajectory may be difficult to realise [24]. Nevertheless, the exceptional increase in body size associated with insular gigantism can result in unexpected morphologies, and evolutionary shifts to novel ecologies in context of the island setting might also be a powerful driver of evolutionary changes in morphology via functional adaptation.

Dormice (Gliridae) are potent exemplars of the evolutionary 'island effect' of body size increase, having evolved extraordinary large sizes more frequently than other mammals –and on at least eight different islands since the beginning of the Miocene [26,27]. Furthermore, giant dormice

52 are known from both the fossil record (e.g. *Hypnomys* spp. from the Balearic Islands and *Leithia* spp.
53 from Sicily and Malta) and an extant population of *Eliomys quercinus* on the island of Formentera [28].
54 Dormice therefore provide an ideal study system for addressing key questions regarding insular
55 gigantism.

56 The fossil giants *Hypnomys* and *Leithia* most likely evolved from a mainland ancestor related
57 to the genus *Eliomys* (Leithiinae) [29,30,31]. Previous studies uncovered craniomandibular differences
58 between extant *Eliomys* populations and fossil island genera [31-34]. The possibility that they were
59 more than simply enlarged forms of their mainland relatives is further supported by the change in
60 ecological niche displayed by the extant giant population on Formentera, which shows increased
61 faunivory in its diet [28]. Furthermore, the morphological features of the extinct island giants imply
62 alternative lifestyles such as increased terrestriality in *Hypnomys* [31] and herbivory in *Leithia* [32].

63 Here, the cranial and mandibular morphology in the extant giant *Eliomys quercinus* from
64 Formentera and the extinct giant genera *Leithia* and *Hypnomys* are investigated in the context of a
65 large dataset of non-giant dormouse skulls. *Eliomys quercinus* has a large geographic distribution
66 across Europe, including several populations on Mediterranean islands. Alongside fossil giants and the
67 extant giant population on Formentera, non-giant *E. quercinus* still display significant intraspecific size
68 variations. We aim to understand the transformation of cranial and mandibular form (size and shape)
69 in giant dormice by investigating the allometric trajectory of non-giant dormice. Characterisation of
70 the common allometric trajectory within *E. quercinus* populations enables us to distinguish between
71 morphological differences occurring due to size variations and those potentially related to other
72 factors. We ask to what extent the cranial and mandibular morphologies of island giant dormice are
73 predicted by extrapolation of the allometric trajectory for extant non-giant dormice, or whether
74 additional morphological variation occurs during evolution of giant size – possibly driven by island-
75 specific shifts in ecology.

76

77 **Material and Methods**

Sample

We analysed the skulls and mandibles of 63 adult specimens (fully erupted third molar) of the extant species *Eliomys quercinus.* Specimens were from the collections of the Senckenberg Museum, Frankfurt (SMF), the Muséum National d'Histoire Naturelle, Paris (MNHN) and the Natural History Museum, London (NHMUK). Table S1 includes a full list of all extant specimens used in this study and details of our µCT scanning methods are given in Appendix S1. Because only adult individuals were analysed, our analyses (see below) describe patterns of static allometry.

Size variation in *Eliomys* was characterised among geographically separated extant populations and in fossil giants. We used centroid size (the square root of the summed squared distances between landmarks and the centroid [35]) derived from our landmark configurations as a size proxy. Our subsequent analyses focused on quantifying allometry within a single species, *Eliomys quercinus*, the closest living relative of insular giant dormice lineages [29,30,31]. Ideally, we would compare extinct giant dormice with their specific mainland ancestor populations. However, phylogenetic relationships among populations of *E. quercinus* are not currently known, let alone the relationships of mainland populations with extinct island giants.

Fossil specimens of the insular species *Hypnomys onicensis, H. morpheus* and *Leithia melitensis* were included in the analyses based on µCT models (Appendix S1), with small missing portions reconstructed from photogrammetric models of other specimens. The fossil specimens include: a composite reconstruction of the skull of *L. melitensis* based on specimens present at the Museo Geologico Gemmellaro (mgupPS 78: 1-5)[32]; the reconstruction of an *L. melitensis* mandible located at the Museo Universitario di Scienze Della Terra, Rome (MUST R2s26); a well preserved skull of *H. morpheus* from Cova des Coral·loides (unnumbered specimen, under the responsibility of the Heritage Authorities of the Consell Insular de Mallorca, Palma); and a mostly complete skull of the giant Balearic dormouse *H. onicensis* in the collection of the Institut Mediterrani d'Estudis Avançats, Esporles, Mallorca (IMEDEA 106855). Although this specimen is likely a sub-adult, based on size, dental wear and the unfused skull sutures, it is the most complete skull available of this species.

104

105 *Shape analyses of extant dormice*

106 Anatomical landmarks were recorded from each cranium (42 landmarks) and mandible (19 landmarks)
107 using Avizo Lite v9.2.0 (Thermo Fisher Scientific, Waltham, MA, USA). The *Arothron* package [36] was
108 used to import the landmarks into R v3.5.3 [37]. We used 3D geometric morphometrics to characterize
109 shape variation among extant populations of *E. quercinus* and extinct giants. Generalized Procrustes
110 Analysis (GPA) was performed, translating the landmark coordinates to the origin, scaling to unit
111 centroid size, and rotating them to a shared orientation, using a least squares criterion [38,39]. This
112 analysis separates variation in size (centroid sizes) from variation in shape (Procrustes coordinates) so
113 they can be treated as individual variables. A Principal Component Analysis (PCA) was performed using
114 the geometric morphometric R package *Morpho* v2.6 [40], in order to evaluate the data in a lower
115 dimensional space and identify the largest variances in shape within the dataset.

116

117 *Allometry*

118 Analysis of variance (ANOVA) was used to test the effect of size on adult shape variation (i.e. static
119 allometry) in *E. quercinus* and the fossil giants. Using the procD.lm() function with 999 iterations in the
120 R package *geomorph* v3.2.0 [41], the following linear model formula was evaluated:
121 $shape \sim log10(size)$, in which size is represented by centroid size. This analysis asks what changes in
122 cranial or mandibular shape are associated with changes in cranial or mandibular size. Our initial
123 analyses included a categorical variable differentiating between non-giant and giant dormice for both
124 the extant dataset (including the extant Formentera giants), as well as the complete dataset (including
125 the fossil giants). When used as a covariate, $shape \sim log10(size) + giant$, this variable asks whether
126 giant dormice show specific differences in skull shape compared to non-giant dormice; when used as
127 an interaction term, $shape \sim log10(size) * giant,$ it asks whether the relationship between shape
128 and size (i.e. its slope) differs between giant and non-giant dormice.

Subsequent analyses aimed to quantify the allometric signal among non-giant populations and therefore used a more restricted sample, excluding giants. The independent effects of population (defined by geographic location) and sex on shape were evaluated for non-giant *Eliomys* specimens using the model: $shape \sim log10(size) + population + sex$ (Tables S2 and S3). We also asked whether the effect of allometry varies among populations (Table S1) using the model formula: $shape \sim log10(size) * population$. The significance of coefficients and interaction terms in these models was assessed using ANOVA with permutation procedures.

Predicted Shape Model

The allometric relationship defined above can be used to evaluate the extent to which the morphology of (giant) specimens is explained by their size. A multivariate regression for allometry $shape \sim size$ can be expressed as $Y = C + BX + E$ [42], in which Y is the shape vector, C is the intercept, B is the vector of the regression coefficients for size and represents the angle of the slope of the multivariate regression line, X represents centroid size, and E explains the error term. When using Procrustes coordinates, the size component X can be evaluated as the difference between the centroid size of each specimen and mean centroid size across all specimens. This procedure renders the intercept term C redundant with the mean shape from Procrustes superimposition.

Our analyses of allometry among non-giant dormice demonstrated a small, but significant, contribution of population (i.e. geographic location) to cranial and mandibular shape variation (Tables S2 and S3). Therefore, we used the allometric relationships derived from the model $shape \sim log10(size) + population$ among non-giant dormice for the allometric base model in the subsequent analyses.

Predicting shape from size.

The base allometric model provides a predicted shape for each specimen based on its size. The Procrustes coordinates of individual specimens can be projected on to an axis described by the vector

of size coefficients, B, from the multivariate regression [43]. This vector defines an axis in multivariate space and is equivalent to the common allometric component (CAC) [44]. The orthogonal projection of specimens onto this axis gives a regression (or CAC) score. The plot of regression score against size provides a 2D representation of the allometric model. Shape residuals describe how the true shape of each specimen differs from its predicted shape and are represented in the plot as the vertical (i.e. shape) deviation of each specimen from the regression line.

Predicting size from shape.

The base allometric model can also be used to infer a 'predicted size' for each specimen based on its shape (Procrustes coordinates). Predicted sizes identify whether the shape of a specific specimen resembles that of a smaller or a larger specimen. They also allow us to infer a best-fit shape based on predicted size, representing the shape a specimen would have if it only deviated from allometric expectations by modification of the position on the allometry line (under the assumption that all shape variation between specimens is associated with allometry).

Predicted sizes were inferred using a custom-written R function: predict.size() (Appendix S2). This function uses the regression vector from the base allometric model to generate a series of predicted shapes representing individuals of different sizes. These predicted shapes are calculated using a 2 x n matrix in which the first row comprises the vector of intercept values and the second row comprises the coefficients of size in the base allometric model. This was multiplied by an $\boldsymbol{m}$ x 2 matrix, in which the first column consists solely of ones and the second column contains an ascending sequence of size values of length $\boldsymbol{m}$. Our predict.size() function by default sets the upper size limit to 1.5 times the size of the largest individual within the dataset. The resulting matrix is transformed to an array based on the number of landmarks within the configuration and its dimensionality, creating a dataset comprising a sequence of shape coordinate data associated with the allometric trajectory per increment of size. This approach can be used to generate predicted sizes of external specimens that

were not included in the base allometric model, provided they are superimposed on the consensus shape of this model.

The extent to which specimen shapes differ from the shapes predicted by allometry, given their predicted sizes, provides a measure of the amount of shape difference between specimen shapes and their deviation from allometric expectations (given actual sizes) that cannot be explained simply by modification of position on the allometry line. It therefore allows us to quantify the amount of non-allometric shape deviation exhibited by a specimen, which might, for example, reflect individual-, population- or species-specific variation. This is calculated as the orthogonal projection of specimen shapes on the regression vector. Our predict.size() function estimates this by evaluating the Procrustes distances between the actual specimen shape and every proposed shape on the regression vector. The proposed shape with the shortest Procrustes distances is the indicator for predicted size.

The relationship between predicted and actual size for each specimen was displayed graphically via a 'predicted size versus actual size', or PSvAS, plot. This method is complementary to existing allometric methods, and allows for the evaluation of the shape of individual specimens with respect to the base allometric model. A line with intercept = 0 and slope = 1 on this plot represents shapes with predicted sizes that match their actual sizes. This identity line divides the graph into two sections, the lower-right indicating specimens with a centroid size exceeding the predicted centroid size based on shape, and the upper-left including specimens with larger predicted sizes than the actual centroid size.

Application of PSvAS to the dormouse dataset

The PSvAS method was used for analysing the shape of giant dormice, based on an allometric base model including non-giant, extant *Eliomys quercinus* specimens. The fit of the fossil and extant giants within the model was analysed to determine whether certain morphological features are in line with the allometric predictions, or can be considered distinct characteristics for giants. Because the giant dormice are considerably different in size and shape compared to non-giant *Eliomys*, including such

specimens will affect the GPA and therefore influence the inferred allometric component. Instead, these specimens were superimposed to the consensus shape of the base model rather than being included in the original GPA.

Results

Shape variation in dormice.

Principal component ordinations for both the cranial and mandibular dataset depict a clear signal related to the distinctive morphology of giant species (Figure 1A,D). The first principal component is correlated with size variation of extant, non-giant populations, with more positive values being associated with larger individuals. The second principal component appears to distinguish between extant (negative values) and fossil (positive values) giants. Overall, these patterns are more defined in the cranial analyses.

Size-shape relationships

Our initial analyses of allometry demonstrate statistical significance for an independent variable distinguishing between giant and non-giant dormice both when including only extant populations, and for the complete dataset including fossil specimens (Tables S4 and S5). This indicates a role for non-allometric shape variation during the origin of giant dormouse cranial and mandibular morphology. The interaction term of this variable is non-significant for the extant dataset, but significant for the complete dataset including fossil specimens. This indicates that the relationship between shape and size among living and extinct giants from multiple islands is different to that among non-giant populations (Figure 1B,E). Our subsequent analyses further interrogate and characterize these differences.

Allometric base model

ANOVAs demonstrate statistically significant effects of size and population on the allometric base models for both mandibular and cranial shape (Tables S2 and S3). The effect of sex (21 females; 24 males; 1 unknown) on mandibular and cranial shape is non-significant and sex was therefore was excluded from further analyses (p = 0.188; p = 0.271). The interaction term between size and population is also non-significant (mandible: p = 0.548; skull: p = 0.346), indicating that there is no evidence for population-specific allometric effects in non-giant dormice. Thus, the best model is: $shape \sim log10(size) + population$; which explains 53% of the total variation in both the mandibular and cranial datasets (Tables S2 and S3). The PSvAS model was used to evaluate the shape of giant dormice crania and mandibles with respect to this allometric model, based solely on non-giant dormice (Figure 1C,F).

Predicted Size versus Actual Size

The PSvAS plots describe the relationship between the size of each specimen and its predicted size based on shape in context of the allometric model (Figures 1C,F and 2). Giant specimens in these graphs are located firmly below the identity line, indicating that their shapes resemble the crania and mandibles of smaller individuals (Table S6). This effect is generally more pronounced for mandibles than for crania (Figure 1). Furthermore, the larger fossil specimens deviate more from the identity line compared to the extant giants from Formentera.

Predicted and actual morphology of giant dormice

Procrustes distances quantify the difference between the actual shape of giants and the predicted shapes based on the allometric model (Table S6). Differences between giant shapes and expectations under the allometric base model are relatively large (cranium: 0.07 – 0.18, mandible: 0.08 – 0.22), especially within the fossil genera *Hypnomys* and *Leithia*. These differences remain large even when using the predicted (best fit) size given shape (Table S6; cranium: 0.07 – 0.13, mandible: 0.06 – 0.12), indicating that the actual morphology of giants is rather poorly predicted by the allometric

model, suggesting that giant dormouse cranial and mandibular morphologies originated via largely non-allometric evolutionary processes.

Based on both their actual and predicted sizes, the crania of larger dormice are expected to have upper incisors that curve more posteriorly, an inferiorly angled rostrum, an increased maximum width of the zygomatic arch, and a relative narrowing of the auditory meatus (Figure 2). The predicted relative narrowing of the auditory meatus is seen in the fossil taxa, but other aspects of the actual shapes of the giants deviate from these predicted shapes: none show the predicted curvature in the incisors, and the proposed inferior angle of the rostrum is only evident in *Leithia melitensis*. The widening of the zygomatic arch is present within fossil giants, but is absent in the extant Formentera giants. Furthermore, the zygomatic widening in the fossil giants is located much more anteriorly than predicted.

Predicted mandibular morphology of giant dormice is also very different from their actual shapes. The predicted shapes show a very narrow and antero-posteriorly elongated structure, whereas the actual giants have robust mandibles, with the posterior part being greatly enlarged dorsoventrally. Although the PSvAS graph implies a best-fit for giant mandibular shapes similar to that of non-giant dormice, the large Procrustes distances between the fitted shape and the actual shape (Table S6) indicate this is not the result of isometric scaling. Instead, the giants exhibit some unique morphologies; e.g. distinct features in *L. melitensis* include a foreshortened and relatively straight lower incisor, an exceptionally large and unperforated angular process, a posteriorly located anterior margin of the masseteric ridge, and a vertically oriented coronoid process.

As the cranial and mandibular warps were created using the respective landmark configurations, features not included in the configuration, such as the shape of the auditory bullae, cannot be reliably assessed using the warped images. Figure S2 shows the positioning of the landmarks on the giants with regards to their predicted shapes. The width of the zygomatic plate, visible in lateral view, seems to increase with size in the fossil specimens. Furthermore, all giants appear to have a

sharply angled cranial vault. Lastly, we noticed a peculiar enlargement of the occipital condyle when observing the µCT scan of *H. morpheus,* not seen in other specimens.

Discussion

Extant giant Formentera dormice and fossil giant specimens of Sicily and Mallorca show substantial craniomandibular differences from their non-giant relatives (*Eliomys quercinus*; Figures 1 and S3). Only a small portion of these morphological differences can be explained by the allometric trajectories of non-giant populations. Insular giant dormice therefore diverge substantially from allometric expectations. Additionally, we recognized that different species of giant dormice show distinctive deviations from their predicted shapes.

Predicting giant size and shape

The cranial and mandibular morphologies of living and extinct island giants are different from those expected under an allometric model. Allometry-related aspects of the shapes of these giants are generally more similar to those of smaller dormice (although they also show substantial non-allometric shape differences), and this effect is more pronounced for the mandible than for the cranium (Figure 1C,F). Although the craniomandibular shapes of giant dormice are more similar to smaller dormice than expected, this does not imply isometric scaling; the actual fit of the giants within the model is rather poor, and is worse for larger specimens (see Procrustes distances Table S6). Phylogenetically, the fossil specimens are more separated from the base model, potentially explaining the poor fit of these shapes within the model. The biologically implausible geometries that result from extrapolation of the allometric model to giant sizes provide an alternative explanation. For example, the predicted skull shape based on the cranial size of *L. melitensis* (log centroid size = 5.02) has an unrealistically flexed cranial vault and occipital region, including a highly constricted foramen magnum. A similarly unlikely morphology is evident for mandibular geometry, with the expected shape at the size of *L. melitensis* (log centroid size = 4.11) being implausible owing to the very thin mediolateral width of the

bone. Interestingly, the morphologies of smaller giants (Formentera population and *Hypnomys*) are not correctly predicted by the allometric base model either. These observations suggest that flattening or truncation of the allometric trajectory occurs at large size in order to maintain biological functionality.

Only part of the morphology of giant dormice can be explained by flattening of the allometric trajectory — large differences are also evident in comparison to their expected shapes based on (smaller) 'best fit' centroid sizes (Table S6; Figure 2). This indicates the presence of population-specific morphological features within island giants, potentially reflecting adaptive variation due to island-specific environmental conditions or ecological shifts. For example, the extant giant population of Formentera is noticeably more faunivorous compared to other populations [28]. This suggests either that insular body size increases have resulted in a dietary niche shift, or that a shift towards carnivory reflects insular selective pressures on Formentera and is the driver of evolutionary increases in body size. Although this is not the classic explanation of large body size in small mammals on islands [1], it indicates that morphological variation among dormouse populations could represent allometry and dietary (or other ecological) adaptations.

Morphological traits of giant dormice

Cranial morphology of island giants clearly deviates from the allometric expectations, even when compared to their 'predicted sizes' (i.e. best-fit sizes to the line of allometry; Figure 2). The robust rostrum and narrowing of the infraorbital foramen within all fossil giants are not predicted by the allometric model at any cranial size. The model predicts the zygomatic arch in giants to become more enlarged posteriorly. In reality, the arch does get more robust, but its maximum width is located much more anteriorly. Larger dormice show a dorso-ventral flattening of the skull and changes to the posterior part of the mandible, such as an elongated coronoid process and enlarged condylar and angular processes. These are areas associated with masticatory muscle attachment [45], and their modification suggests relative increases in molar bite force [46,47] or gape [48,49]. Multiple studies

have already shown that small changes in cranial and mandibular size and shape can affect mechanical advantage and gape, both of which will impact the range of dietary items that can be processed. This effect has been shown in a number of mammalian groups [50-53] but is particularly well-studied in rodents [54-60]. The flattening of the skull is commonly seen in more rupicolous dormice [61], although it may also be product of enlarged body size owing to negatively allometric scaling of brain size [62] and craniofacial evolutionary allometry (CREA)[63]. This pattern, which is seen in many mammalian groups, predicts relatively smaller braincases and longer rostra in larger species [64,65].

Unique features of giant dormouse species

Significant modifications to shape and size can result from evolutionary adaptation to novel ecologies, including new diets [22]. We therefore interpret the unique morphological features identified in the giant dormouse populations as reflecting specific ecological adaptations to insular settings. As well as diverging from the non-giant allometric trajectory, giant dormice also differ morphologically from one another. Such differences can be the result of various factors, including variation in ecosystem composition, ecological niche occupation, as well as duration of isolation on islands. The introduction of *Eliomys quercinus* to Formentera is thought to have occurred roughly 4000 years ago, whereas both *Hypnomys* and *Leithia* were isolated for millions of years. Even though the morphology of Formentera dormice does not resemble an intermediate shape between an average-sized *E. quercinus* and the fossil giants, the differences in duration of isolation are substantial. Many population-specific aspects of giant dormouse cranial, and especially mandibular, structure complement previous evidence of divergent dietary and other ecological traits in these taxa.

Formentera

The Formentera dormice are the only extant giants and are morphologically different from the fossil giants. It is the only giant population retaining a large infraorbital foramen. Furthermore, the mandibular morphology of this population is characterised by a deep angular notch and relatively large

coronoid process, in contrast to the fossil giants. This enlarged coronoid results in a larger attachment area for the temporalis muscle, suggesting an increased incisor bite force, which would be advantageous for the extensive faunivorous behaviour observed within the Formentera population [28]. Previous research has suggested that faunivory, more than other diets, places unique pressures on rodents, driving greater morphological change [59,66]. However, this is not the case in the dormice studied here, with the Formentera population resembling non-giant dormice more than the other giants, based on the relatively short Procrustes distances of the best-fit in the PSvAS model (cranium 0.07; mandible 0.06) (Table S6).

Hypnomys

The *Hypnomys* material in our dataset is much more robust than other dormice, with the exception of *Leithia melitensis.* The PSvAS model indicates that the morphology of this genus is substantially different from extant dormice (cranium 0.10; mandible 0.08). The *H. onicensis* specimen examined here is considered a subadult and is less robust than *H. morpheus.* The latter is characterised by exceptionally pronounced occipital condyles. The robust morphology of the zygomatic area and mandible in the two *Hypnomys* specimens indicates well developed masseteric musculature, which suggests a diet including tough foods for this genus. A more abrasive plant-based diet has also been suggested based on molar microwear [67].

Leithia

Leithia melitensis is the largest and most robust dormouse. *Hypnomys* and *Leithia* show similar morphological modifications, although these are often more pronounced within *Leithia* [32]. This also explains the relatively large Procrustes distances seen in the PSvAS model for this species (cranium 0.13; mandible 0.12). In particular, the width of the rostrum and the zygomatic plate is exceptional. The mandible within this giant has very large angular and condylar processes. It is the only giant in which there appears to be no fenestration of the angular process. However, the functional significance

386 of this fenestra is unknown. The coronoid is deflected less posteriorly, resulting in a more upright
387 position. The anterior margin of the masseteric ridge is positioned more posteriorly than in other
388 dormice and the incisor is relatively short and curves less superiorly. The cranial and mandibular
389 features seen in *L. melitensis*, in particular the exceptionally robust mandible, likely represent
390 adaptations to a herbivorous diet [68], possibly explaining its extraordinary size. In addition,
391 considerable variability in wear of the molar row is seen within the analysed fossil material of *L.*
392 *melitensis* (Figure S4), indicating a relatively abrasive diet against which the molars were used
393 extensively, also consistent with herbivory.
394
395 *Conclusion*
396 Multiple, independent dormice lineages achieved exceptional large size in insular habitats since the
397 end of the Messinian Salinity Crisis (5.33 Ma [69]). Extrapolation of common allometry as an
398 evolutionary line of least resistance on short timescales predicts that island giants could have highly
399 similar craniomandibular morphologies. Moreover, a graded trend to gigantism as proposed by the
400 island rule suggests that the importance of selective pressures within an ecosystem varies in a
401 predictable manner [13,14]. However, we find that the morphologies of giant dormice are not an
402 extrapolation along the allometric gradient of non-giant populations. This indicates that insular
403 gigantism may lead to a deviation from the otherwise strong allometric conservatism suggested to
404 exist in rodents [70]. Furthermore, the cranial and mandibular features of giant dormice contain a
405 prominent population-specific component, illustrating divergence and inherently non-predictable
406 adaptations to various different ecological niches, on different islands. These differences in the
407 evolutionary pathways of island giants may reflect differences in ecosystem composition among
408 islands and through geological time. Our findings have implications that extend beyond the study of
409 giant dormice, suggesting that island adaptation may commonly involve ecological shifts that are
410 unique and context-dependent, resulting in a high diversity of evolutionary responses to insular
411 habitats in mammals.

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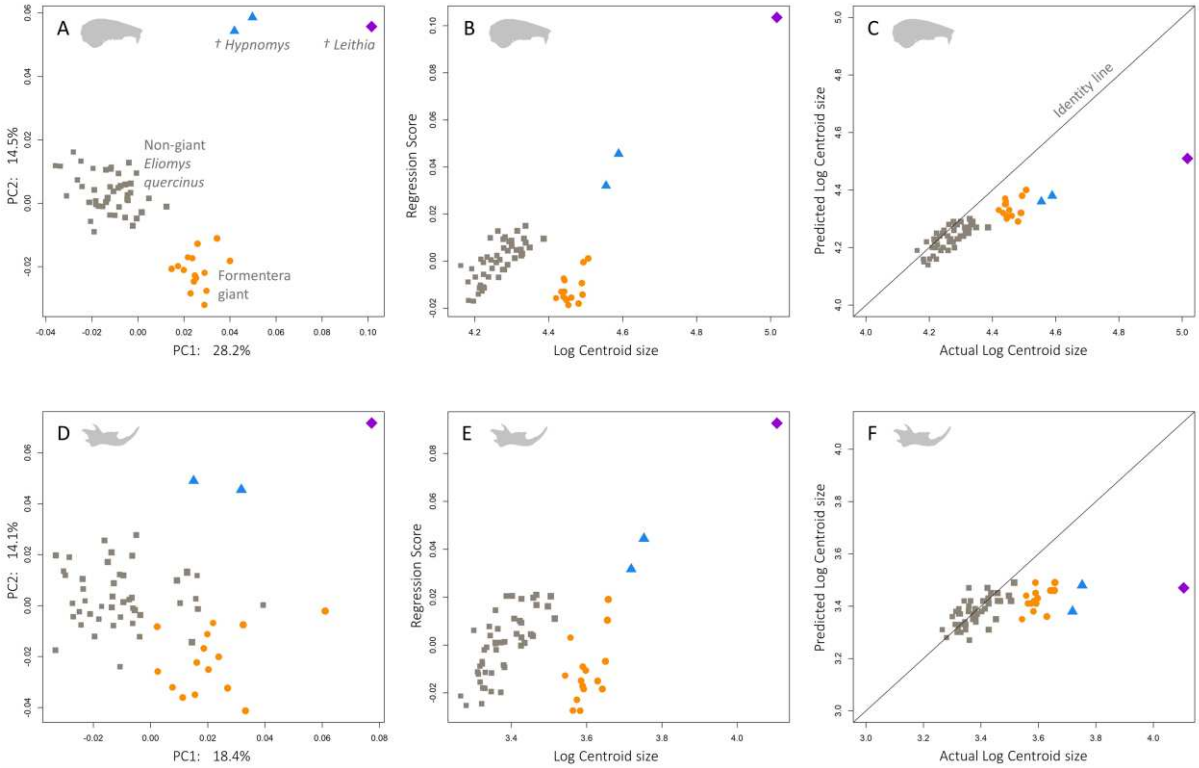
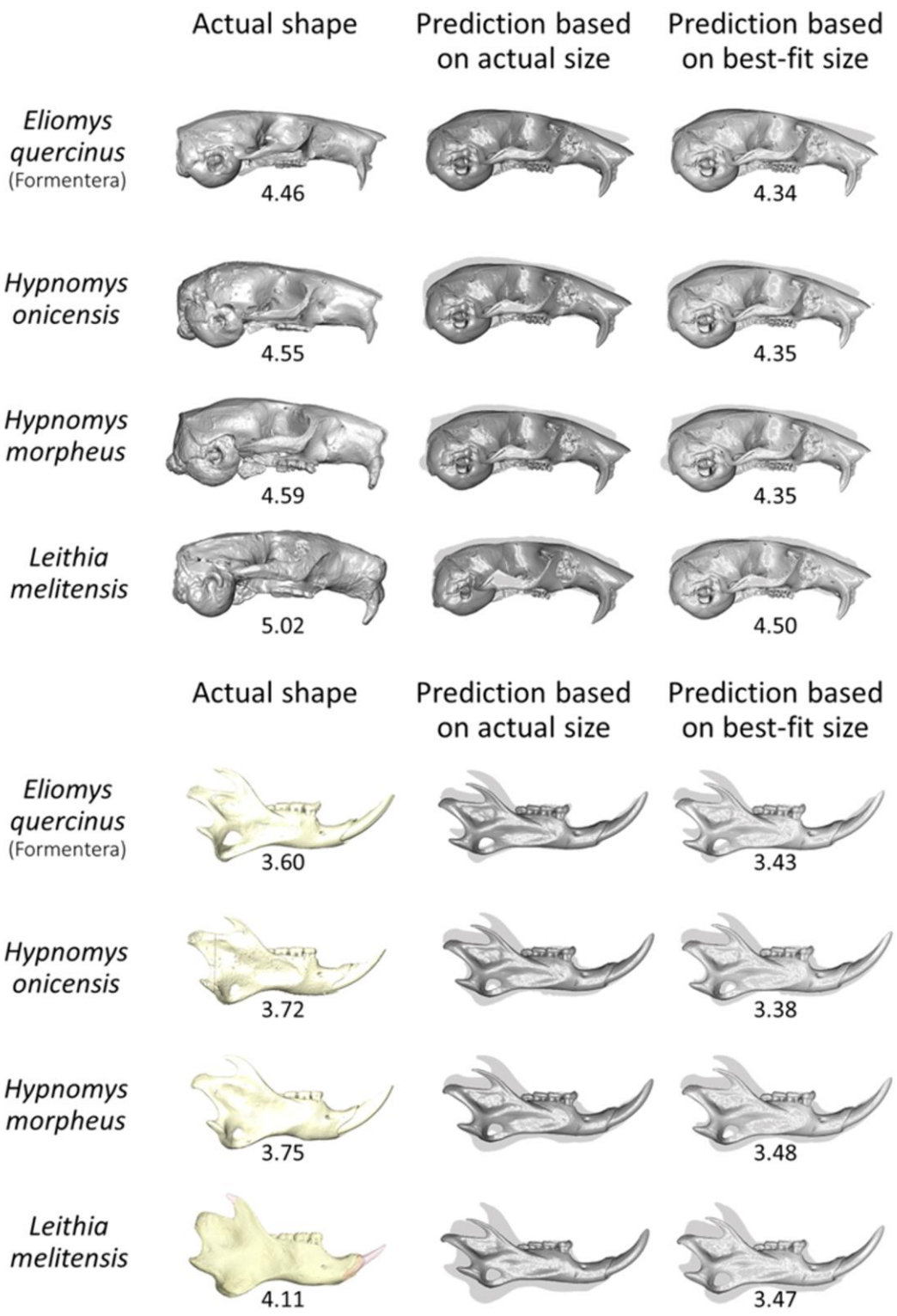


Figure 1: Cranial (top) and mandibular (bottom) shape differentiation in extant *Eliomys quercinus* specimens and fossil giants on the first two principal components (A,D); the common allometric component versus log centroid size with grouping (B,E); and the predicted size versus actual size analyses based on a non-giant base model including the predicted sizes for the giant Formentera population and fossil giants (C,F).



610

611 Figure 2: Predicted shapes of the fossil giants derived from the PSvAS model, using the shape

612 predicted by the actual centroid size of the specimen and the shape presumed to be the best fit with

613 the actual shape of the specimen.